

NEST PREDATORS OF OPEN AND CAVITY NESTING BIRDS IN OAK WOODLANDS

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ABSTRACT.—Camera setups revealed at least three species of rodents and seven species of birds as potential predators at artificial open nests. Surprisingly, among avian predators identified at open nests, one third were Bullock's Orioles (*Icterus bullockii*). Two rodent species and three bird species were potential predators at artificial cavity nests. This high predator diversity was consistent with previous studies, although the number of avian predators at open nests was higher than expected. Received 31 March 1998, accepted 22 Nov. 1998.

As the primary source of nest failure among birds (Lack 1968, Ricklefs 1969), predation is a likely factor affecting species' coexistence, habitat selection, and conservation (Zimmerman 1984; Martin 1988a, b). When nest predation differs among species, habitats, and locations, it can influence life history traits such as clutch size, nest placement, developmental period, and number of broods (Ricklefs 1969; Martin 1988c, 1995). Avian ecologists generally agree that predation rates differ among species nesting in cavities and open (cup) nests (Lack 1954, Nice 1957, Ricklefs 1969). Predators may differ as well, but little is known about predators of bird nests because predation is rarely observed, and observations are biased toward diurnal predators. Some researchers have made assumptions about broad classes of predators based on the appearance of the depredated nest, but few data exist to support those assumptions, and authors disagree on evidence used to assign depredated nests to predator groups and the reliability of the evidence (Best 1978, Best and Stauffer 1980, Wray et al. 1982, Boag et al. 1984, Hernandez et al. 1998a, Marini and Melo 1998). Here we report results of a camera study at both artificial open and cavity nests. The primary objective of our study was to identify nest predators as part of a larger study of reproductive success among birds in oak-pine woodlands in the west-central foothills of the Sierra Nevada of California.

STUDY AREA AND METHODS

The study was done at the San Joaquin Experimental Range, approximately 40 km north of Fresno, Cal-

ifornia. The San Joaquin Experimental Range covers about 1875 ha and ranges in elevation from 215 to 520 m. Climate is Mediterranean, with cool, wet winters and hot, dry summers. A sparse woodland overstory of blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*) covers most of the San Joaquin Experimental Range. A scattered understory of shrubs includes mainly wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), redberry (*Rhamnus crocea*), and mariposa manzanita (*Arctostaphylos viscida mariposa*). The San Joaquin Experimental Range has been lightly to moderately grazed since about 1900 and is surrounded on all sides by similar habitat.

Using nests of California Towhees (*Pipilo crissalis*) collected at the end of the previous field season, we situated artificial open nests low in small trees or shrubs in positions similar to those known to be used by California Towhees (on a forked branch or supported by several twigs). At cavity setups, eggs were placed with a "pick-up" tool, using cavities known to be deep enough for cavity-nesting species at the San Joaquin Experimental Range. Most cavities were excavated by primary cavity nesters, but some natural cavities previously used for nesting were also used. A fiberscope (Purcell 1997) was used to guide the placement of eggs in cavities, to monitor eggs for possible predation, and to measure cavity depth. To avoid leaving olfactory cues at nests, field personnel washed their hands before going into the field with a soap developed to remove human scent and sprayed their boots with a scent masker. We avoided dead-end trails and did not create paths that might lead predators to nests.

One experimental egg was placed in open nests, and one or two eggs were placed in cavity nests, the number and type depending on availability. Most eggs used in open nests were from wild House Sparrows (*Passer domesticus*) or captive Ringed Turtle-Doves (*Streptopelia risoria*); most eggs in cavities were from captive Zebra Finches (*Poephila gullata*). We sometimes used a Buttonquail (*Turnix* sp.) egg as the second egg in a cavity nest. House Sparrow eggs were slightly smaller and Ringed Turtle-dove eggs slightly larger than those of California Towhees (see Baicich and Harrison 1997). Although similar in size to eggs of the Plain Titmouse (*Baeolophus inornatus*), the Zebra Finch

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eggs were smaller than eggs of all cavity-nesting species in our study area.

Predation at open nests was monitored mechanically, with an egg encircled by a loop of wire attached within a nest of the California Towhee. Removal of the egg activated an electrical signal to a solenoid, tripping a camera mounted nearby. We used inexpensive, autofocus, autoflash, Keystone 550D or 590AF cameras, allowing identification of both diurnal and nocturnal predators. (Trade names and commercial products are mentioned for information only; no endorsement by the U.S. Department of Agriculture is implied.) Details on the mechanical system for open nests are available from KLP. At cavity nests, we used Trailmaster Active Infrared trail monitors with weatherproof, autoflash 35 mm cameras to monitor predation. One box that transmitted (12.1 cm L \times 8.3 cm W \times 4.6 cm D) and one that received (19.1 cm L \times 8.9 cm W \times 5.3 cm D) the infrared beam were placed on each side of the cavity so that an animal entering it would break the beam, triggering the camera positioned on a nearby branch with a good view of the cavity. Because Trailmaster units are designed to be set up horizontally across trails, we modified the boxes so they could be attached easily to the tree bole or limb with bungee cords. Sensitivity was set at the minimum delay of 0.5 s (one pulse) before an event was recorded, and the camera delay between photos was set at the minimum of 6 s.

Based on the nesting seasons of cavity- and open-nesting species, cameras were set up from March through June 1995 (cavities) and April through June 1995 (open). We used 10 open-nest setups to monitor 70 open nests, and 7 Trailmaster monitors at 61 cavity nests. Some data on cavity nests were also included from the 1993 and 1994 field seasons (eight each year). All setups were checked about every 4 days. If an egg was taken, or not taken after 14 days, the setup was dismantled and moved to another location and installed using fresh eggs.

All artificial nests of the same nest type were separated by at least 200 m in an effort to reduce the chance of visitation by the same animal at two or more setups. This distance was thought to be enough to assure independent samples of the small mammals identified as predators in this study. Based on spot mapping at the San Joaquin Experimental Range (unpublished data), territories of the Western Scrub-Jay (*Aphelocoma californica*), a common nest predator, were approximately 120–210 m in diameter. Mean territory diameters of other common bird species ranged from 180 m (California Towhee) to 310 m (Western Kingbird, *Tyrannus verticalis*). Some cavity setups were closer than 200 m to open set-ups, but cameras and eggs were not placed concurrently at the two nest types.

At open nests, we measured nest height and the height and diameter of the shrub or small tree containing the nest. Diameter was measured as the mean of the maximum crown diameter and the widest diameter perpendicular to the maximum diameter. At cavity

nests, we measured nest height, cavity depth, and horizontal and vertical entrance diameters. We tested differences in these attributes between predated and unpredated nests using two-tailed *t*-tests (SAS version 6.12 for Windows, SAS Institute 1988), $\alpha = 0.05$, and Bonferroni adjustments for multiple tests. We calculated power according to Abramowitz and Stegun (1964) based on specified effect sizes, an α of 0.05, and two-tailed tests using an inhouse SAS program.

RESULTS

Open nests.—Eggs were removed from 39 of the 70 open nest setups, but we could identify the animals at only 29 of those. Rodents were identified at four (14%): deer mouse (*Peromyscus* spp., two cases), California ground squirrel (*Spermophilus beecheyi*, one case), and Merriam's chipmunk (*Eutamias merriami*, one case). At least five bird species were photographed at the remaining 25 nests (86%) from which an egg was taken: Western Scrub-Jay (12 cases), Bullock's Oriole (*Icterus bullockii*, 7 cases), Acorn Woodpecker (*Melanerpes formicivorus*, 1 case), Western Kingbird (1 case, a pair), and California Towhee (1 case). We could not identify the bird species at the three remaining setups.

In three additional cases, eggs were pecked, chewed, or otherwise damaged but not removed. A pair of Plain Titmice pecked a large hole in the egg at one nest; a female Brown-headed Cowbird (*Molothrus ater*) punctured the egg in another nest; and either a dusky-footed woodrat (*Neotoma fuscipes*) or a Western Scrub-Jay chewed or pecked another egg (both species were photographed).

We may have underestimated nocturnal predation. Only one photo of a deer mouse was taken at night. In 2 of the 10 cases with no identifiable predator, photos were taken at night but were dark, perhaps because the camera's flash was too far from the nest or failed to operate properly (see also Hernandez et al. 1998b).

No attribute measured at open nest setups differed significantly between predated and nonpredated nests (Table 1; $P > 0.05$ in all cases, $P < 0.017$ required for Bonferroni adjustment for multiple tests).

Cavity nests.—Photos were taken at 47 of 69 cavity nests where the egg was removed or pecked open. Interpretation of the photos was complicated, however. First, the minimum camera delay did not allow a photo each

TABLE 1. Nest site variables and results of *t*-tests for nonpredated ($n = 18$) and predated ($n = 48$) open nests at the San Joaquin Experimental Range.

	Nonpredated open nests Mean (SE)	Predated open nests Mean (SE)	P^a	Power
Nest height (m)	1.21 (0.11)	1.11 (0.06)	0.48	0.97 ^b
Substrate height (m)	4.61 (0.81)	4.25 (0.41)	0.67	0.91 ^c
Substrate diameter (m)	6.03 (1.34)	4.90 (0.40)	0.43	0.82 ^c

^a A *P*-value of 0.017 is needed for significance at $\alpha = 0.05$ after Bonferroni adjustment for multiple comparisons.

^b Based on an effect size of 0.5m.

^c Based on an effect size of 3 m.

time the infrared beam was broken after an initial photo was taken. Consequently, photos rarely showed animals leaving a cavity nest and none showed one "caught in the act" of leaving with an egg. We had to assume that an animal in a photo consumed the missing egg. Second, in seven cases the egg was gone and no animal was evident in the photo (see also Brooks 1996). The departure of some predators from a cavity may have been too rapid for it to be caught in the photo, or photos with no animal may have resulted from direct sunlight entering the receiver window (Kucera and Barrett 1993). Third, in 15 instances more than one species entered the cavity and tripped the camera before we found that the egg was gone. Fourth, in 16 cases nest material was added to the cavity by birds or mammals so we could not ascertain whether the eggs had been eaten or simply buried. We did not include these cases in our comparisons of predated and nonpredated nests.

In nine cavity setups with missing eggs, only one species appeared in the photos. The assumed predators were European Starling (*Sturnus vulgaris*; four cases), House Wren (*Troglodytes aedon*; one case), Western Blue-

bird (*Sialia mexicana*; one case), deer mouse (one case), and unidentified squirrels (probably California ground squirrels; two cases). All photos were taken during daylight hours except that of the deer mouse.

No attribute measured at cavity nests differed significantly between predated and nonpredated nests (Table 2; $P > 0.05$ in all cases, $P < 0.01$ required after adjusting for multiple tests).

DISCUSSION

Our results are consistent with other studies using artificial nests in finding a high diversity of nest predators, ranging from six to nine species (Henry 1969, Wilcove 1985, Reitsma et al. 1990, Leimgruber et al. 1994). We identified eight species at open nests, and two (possibly three) other species pecked or pierced eggs. Picman and Schriml (1994) found only one or two major predator species in each of four vegetation types, although predator diversity ranged from four (marsh) to nine species (scrubland and forest). Lack of independence of the setups in their study may have overestimated the importance of some predator species (see below). Interestingly, all

TABLE 2. Nest site variables and results of *t*-tests for predated and nonpredated cavity nests at the San Joaquin Experimental Range.

	Nonpredated cavities		Predated cavities		P^a	Power
	Mean (SE)	<i>n</i>	Mean (SE)	<i>n</i>		
Nest height (m)	3.82 (0.24)	35	3.78 (0.23)	32	0.90	0.98 ^b
Depth (cm)	25.1 (1.94)	35	31.0 (2.42)	31	0.06	0.95 ^c
Vertical entrance diameter (cm)	5.68 (0.67)	34	5.06 (0.16)	30	0.37	1.00 ^d
Horizontal entrance diameter (cm)	5.19 (0.19)	34	5.14 (0.13)	30	0.83	0.98 ^d
Minimum entrance diameter (cm)	4.80 (0.15)	34	4.94 (0.14)	30	0.51	0.99 ^d

^a A *P*-value of 0.010 is needed for significance at $\alpha = 0.05$ after Bonferroni adjustment for multiple comparisons.

^b Based on an effect size of 1 m.

^c Based on an effect size of 0.5 cm.

^d Based on an effect size of 1.0 cm.

but one (Acorn Woodpecker) of the avian predators at open nests in our study were open nesters and all avian predators at cavity nests were cavity nesters.

We know of only two efforts to study predation at experimental cavity nests (Wilcove 1985, Sandström 1991), neither of which identified predators. Although some species photographed at our cavity setups may have been only reconnoitering potential nest sites, they may also opportunistically eat eggs thus encountered in a cavity. The importance of birds as predators at active cavity nests, defended by nesting birds, is unknown but probably significant in some instances. European Starlings are known to usurp nest sites from other bird species (Troetschler 1976, Ingold 1989) and, although the contents of the cavities were unknown, eggs were likely present in some when usurpation occurred late enough in the nesting cycle for egg-laying or incubation to have begun. Our results suggest that starlings probably consume eggs in the course of usurping nest sites.

Although several species of corvids are believed to be important predators at open nests (Yahner and Wright 1985, Yahner and Scott 1988, Andrén 1992, Picman and Schriml 1994, Hannon and Cotterill 1998), nest predation at open nests by noncorvids has not often been documented. Gates and Gysel (1978) reported anecdotal evidence of nest predation by an Eastern Screech-Owl (*Otus asio*). Picman (1987) photographed Marsh Wrens (*Cistothorus palustris*), House Wrens, and Gray Catbirds (*Dumetella carolinensis*) predating nests. Picman and Schriml (1994) recorded predation events by Broad-winged Hawks (*Buteo platypterus*), Eastern Meadowlarks (*Sturnella magna*), and Red-winged Blackbirds (*Agelaius phoeniceus*). The Marsh Wren was the only predator recorded at nests of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Picman and Isabelle 1995). Predation of open nests by woodpeckers has been documented rarely (Bent 1939; Watt 1980; Hernandez et al. 1998a, b; Robert Cooper, unpubl. data), and never by the Acorn Woodpecker. Egg removal by Bullock's Orioles was surprisingly common in this study. Both sexes of this oriole are known to be ejectors of Brown-headed Cowbird eggs, and they sometimes consume the eggs before removing

the shells (Sealy and Neudorf 1995). Although some of these "predators" may destroy nests or eggs with no nutritional motivation, predation of open nests by noncorvids may be more frequent than previously thought.

Leimgruber and coworkers (1994) and Picman and Schriml (1994) also found that potential predators visiting nests did not always eat the eggs. Consistent with the findings of Picman and Schriml, mammals in our study nearly always took the egg. Picman and Schriml (1994) classified as "accidental visitors" several bird species that visited nests, including Red-winged Blackbirds, that apparently ate eggs at 6 of 29 nests visited. Regardless of motivation, the effect of egg removal on the nesting birds is the same.

Artificial nest studies are just that—artificial; some biases are certainly involved (Martin 1987, Reitsma et al. 1990, Whelan et al. 1994, Marini and Melo 1998, Wilson et al. 1998). As visual predators, birds may key in on cameras or unrealistic nest placements, or they may follow field workers and learn to associate conspicuous markers at nests with food (Picozzi 1975, Götmark 1992). At open nests we were able to attain a realistic nest placement or a good camera view, but usually not both. At cavity nests, the transmitters and receivers may have inhibited predators from going to a cavity or may have attracted curious predators. Predation also may have been more or less likely at artificial nests than real nests defended by adult birds, but even real nests are left unattended at regular intervals. In spite of these potential biases, we feel that useful data can be obtained from studies of artificial nests because they establish baseline data in an arena where so little is known.

We believe that the value of studies using artificial nests can be substantially increased if studies are designed more carefully to reduce potential biases. For example, most of the studies we reviewed used distances between setups ranging from 20 to 60 m. Such short intervals risk detection of the same individual predator at two or more setups, violating assumptions of independence. Ideally, the distance between artificial nests should exceed the largest home-range diameter of the suite of likely predators. One might argue that shorter distances are appropriate for examin-

ing predation rates, although rates from artificial nest studies are of questionable value for extrapolation to natural conditions (Martin 1987, Whelan et al. 1994, Wilson et al. 1998). Replication over large areas is required to characterize the suite of predators for a given vegetation type, since predators are often unevenly distributed in space and time.

Further problems of independence may have occurred in studies that replaced eggs in nests that had been predated previously. Nour and coworkers (1993) suggested that such egg replacement may not be a problem in studies using plasticine eggs or eggs made from modeling clay because the eggs are not eaten and provide the predator no incentive to return, although predators could avoid nests with clay eggs because of prior negative conditioning.

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